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It is well documented, in the biological literature, that many species throughout the animal kingdom, exhibit Gompertzian or Weibull-like population level survival distributions. Many researchers have long assumed, believed, or otherwise postulated that an individual organism in such a population, survived according to an exponential survival distribution. Using well-known results from reliability theory, it is shown that if every individual in the population is exponentially distributed, then a Gompertzian or Weibull group/population dynamics (or any other dynamics with a strictly increasing mortality rate for some interval) is not possible. This implies that, for species with a population level Gompertzian or Weibull (with the mortality rate strictly increasing) survival curve, some or all of the individual organisms must have nonexponential lifespans.

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A Population of Exponentially Distributed Individual

Lifespans Cannot Lead to Gompertzian or to

Weibull (with Increasing Mortality Rate) Dynamics

by

Frank Guess[*]

Department of Statistics

University of South Carolina

Columbia, SC   29208

        and

NCSU Box 8203

Department of Statistics

NC State University

Raleigh, NC   27695-8203

Matthew Witten[+]

[+]Department of Community Health,
School of Medicine
        and
Department of Engineering
Mathematics and Computer Science,
Speed Scientific School

University of Louisville

Louisville, KY   40292

Guess and Witten

ABSTRACT

It is well documented, in the biological literature, that many species throughout the animal kingdom, exhibit Gompertzian or Weibull-like population level survival distributions. Many researchers have long assumed, believed, or otherwise postulated that an individual organism, in such a population, survived according to an exponential survival distribution. Using well-known results from reliability theory, it is shown that if every individual in the population is exponentially distributed, then a Gompertzian or Weibull group/population dynamics (or any other dynamics with a strictly increasing mortality rate for some interval) is not possible. This implies that, for species with a population level Gompertzian or Weibull (with the mortality rate strictly increasing) survival curve, some or all of the individual organisms must have nonexponential lifespans.

Guess and Witten

Th.. biological literature is replete with illustrations of various
species of organisms that exhibit Gompertzian, Weibull or Gompertzian like
survival distributions (Figures 1-2, Comfort (1), Witten (2-4) for examples).
The assumption has long been held, among researchers, that an individual
organism-in a population-survives according to an exponential survival
distribution. That is, if S(t) is the probability that an individual
survives past time t, then S(t) is of the form

$$S(t) = e^{-\lambda t} \tag{1}$$

where λ is the inverse of the expected lifespan. Each individual, in the
population could, of course, have a different mortality rate (5).

Exponential survival distributions are derived from the assumption of
constant mortality rate (failure rate). This assumption is equivalent to the
statement that the probability of an organism's survival until time $t + \Delta t$,
given its survival until time t, is constant for all time t. That is, the
per capita death rate λ given by

$$-\frac{1}{N}\frac{dN}{dt} = \lambda \tag{2}$$

is a constant. Given the known classes of experimental survival curves, it is
useful and important to address the question of whether or not one can derive
a Gompertzian lifespan distribution from some mixture (population) of
individuals having exponential survival (lifespan) curves. That is, can a
population of exponential survival distributions, at the individual level,
give rise to a Gompertzian or Weibull-like population dynamics?

Proschan (7) considered a naturally occurring mixture of exponentials in
the aircraft industry (Cf. also, for example, (8), (9), (10) and (11) for
more on mixtures). Proschan demonstrated that a survival distribution

Guess and Witten

arising from any mixture of exponentials will always possess a <u>decreasing</u> mortality rate (DMR). That is, it will process a decreasing failure rate (where by decreasing we mean nonincreasing). The Weibull-like populations that have been empirically observed are observed to have a strictly increasing mortality rate. Gompertzian populations always have a strictly increasing mortality rate. Given the result of Proschan (7), it is therefore not possible to obtain a Gompertzian or Weibull-like population dynamics from any mixture of individual exponential lifespans; as such a survival distribution implies the existence of a strictly increasing mortality rate. (It is possible, however, for a mixture of exponentials to yield a Weibull with a DMR, e.g., see (10), for neonates a DMR is plausible, but for older organisms it is not.)

The biological import of this statement is that some or all of the individual lifespans, comprising the population, must be nonexponential in their survival behavior. This result will also be the case, more generally, for any population survival distribution with a strictly increasing mortality rate over the entire lifespan or, more restrictively, even only on some subinte.val of the lifespan (e.g., for all ages t such that $t \geq t_o$ for t_o a large enough age). A simple illustration of such a population would be in which there was both neonatal and post-neonatal death (Witten (4)). Here, one mixes exponential and Gompertzian distributions to describe the known population dynamics (Figures 3-4). That is, again some or all individual lifespans will have to be nonexponentially distributed to yield the empirically observed population dynamics.

References and Notes

1. A. Comfort, The Biology of Senescence (Elsevier/North Holland, NY, 1979).

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5. One possible means of addressing this issue is to assume that there is some type of distribution $\lambda(t)$ of mortality rates such that $E[\lambda] = \lambda_D(t)$ a deterministic function and that $\lambda(t)$ is perturbed by a mean zero, variance σ^2, white noise (or colored noise) process. This gives rise to a stochastic differential equation for the survival distribution $S(t)$ (see Witten (6) for discussion and further references).

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11. M. Hollander and F. Proschan, in Handbook of Statistics, Vol. 4, Nonparametric Methods, P. R. Krishnaiah and P. K. Sen, Eds. (North-Holland, Amsterdam, 1984), pp. 613-655.

12. We gratefully thank F. Proschan for introducing us to each others work. F. G. expresses appreciation to F.Proschan and the Reliability Center at

Guess and Witten

Guess and Witten

LEGENDS FOR FIGURES

Figure 1:   Percent survival of Cynolebias adoloffi. Reproduced from
            Comfort (1).

Figure 2:   The effects of NDGA-feeding on survival, in male and female
            mosquitos. Reproduced courtesy of C. Lang.

Figure 3:   Survival curves for United States females in the years 1900, 1960,
            and 1980. Notice the early neonatal dip in all of these curves.
            Reproduced courtesy of the author K. Manton.

Guess and Witten

Figure 4: An illustration of the wide variety of dynamics embedded in a two

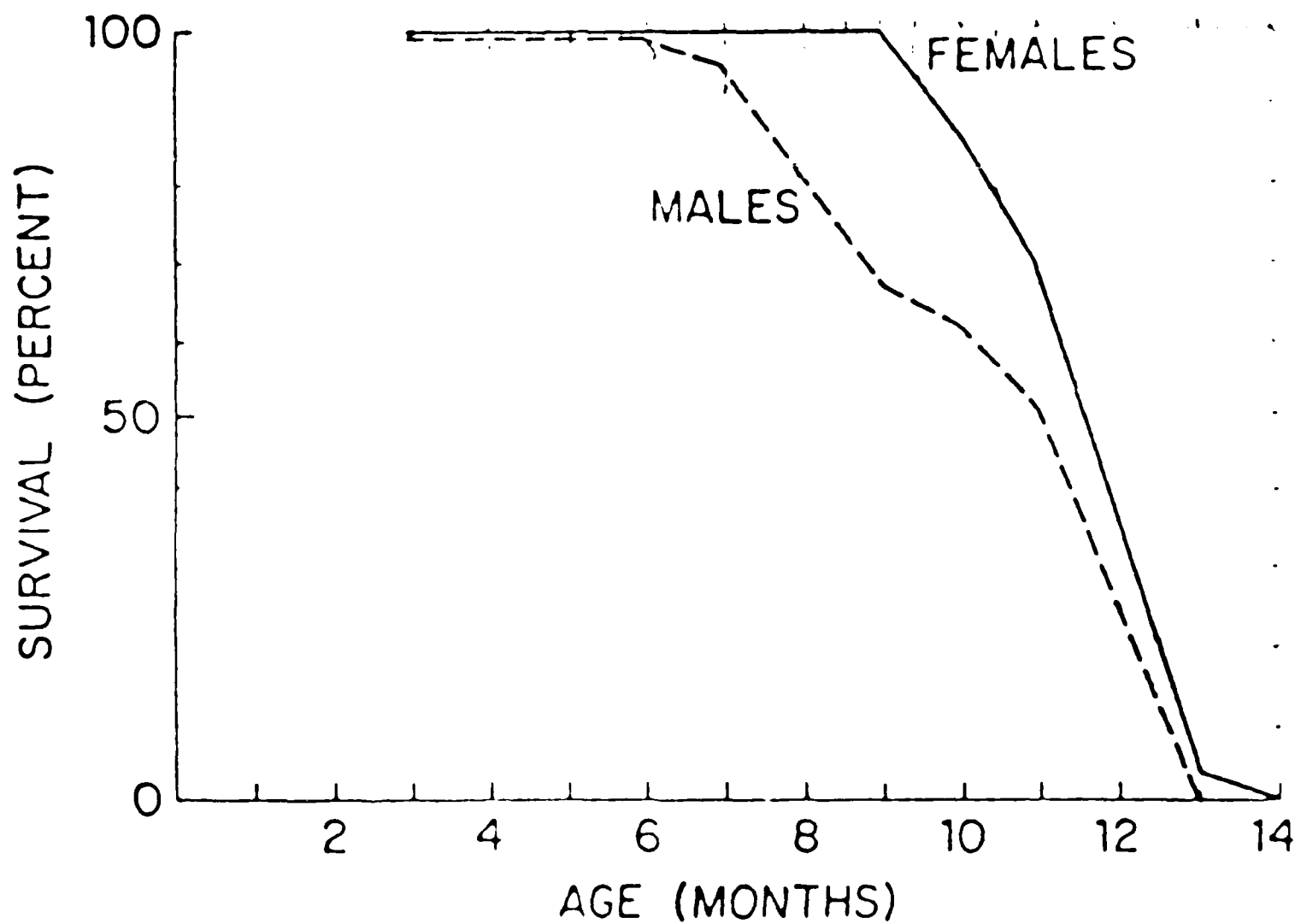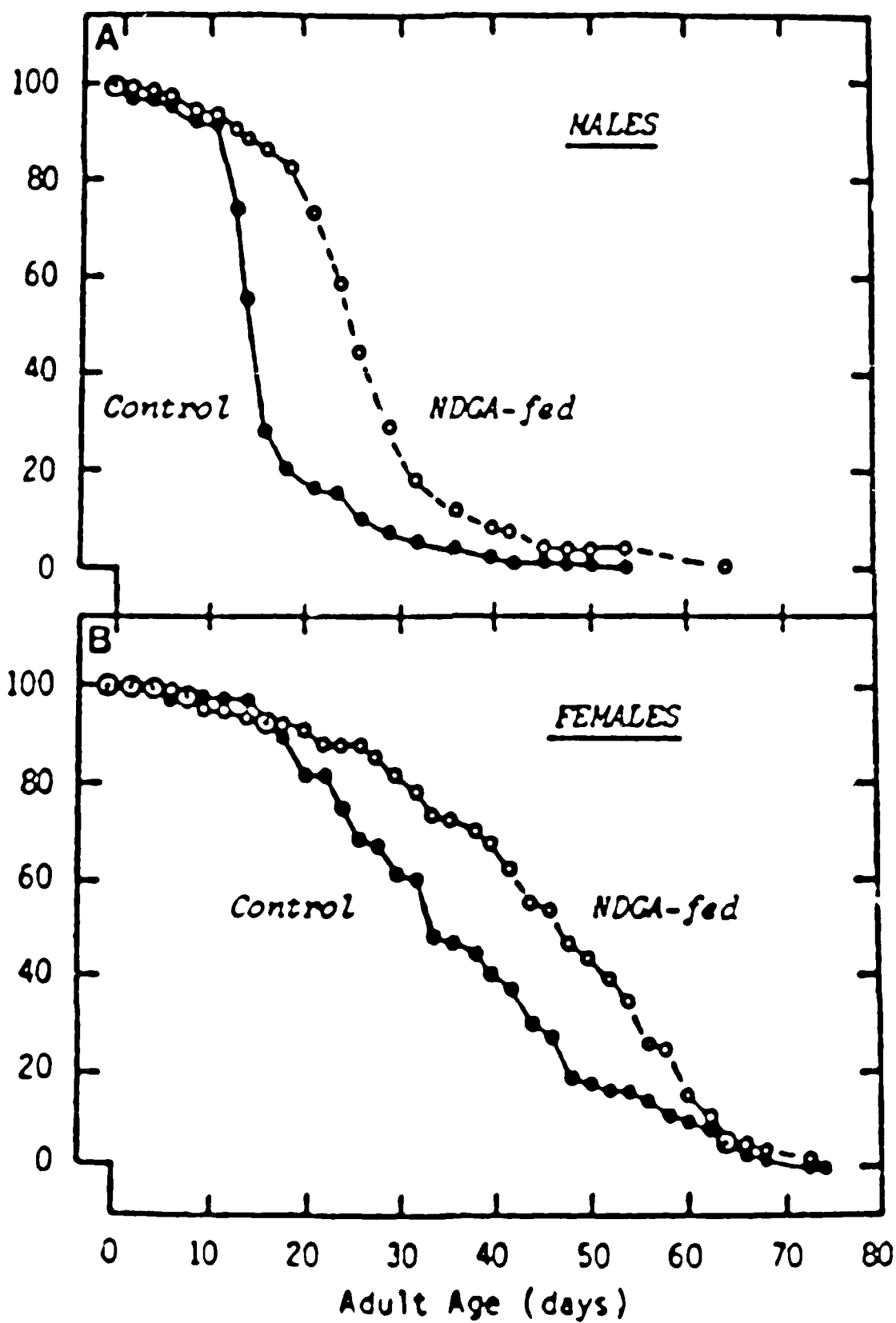group population model. Reproduced from Witten (4).

Figure 1

Adult Age (days)
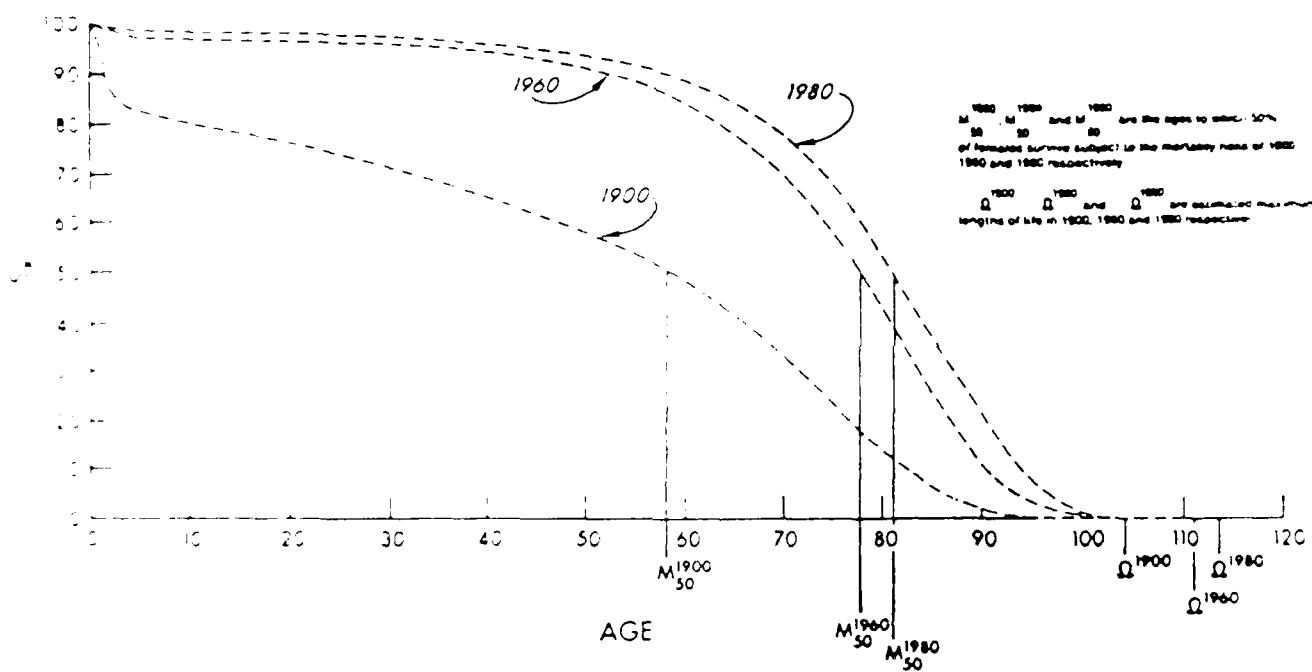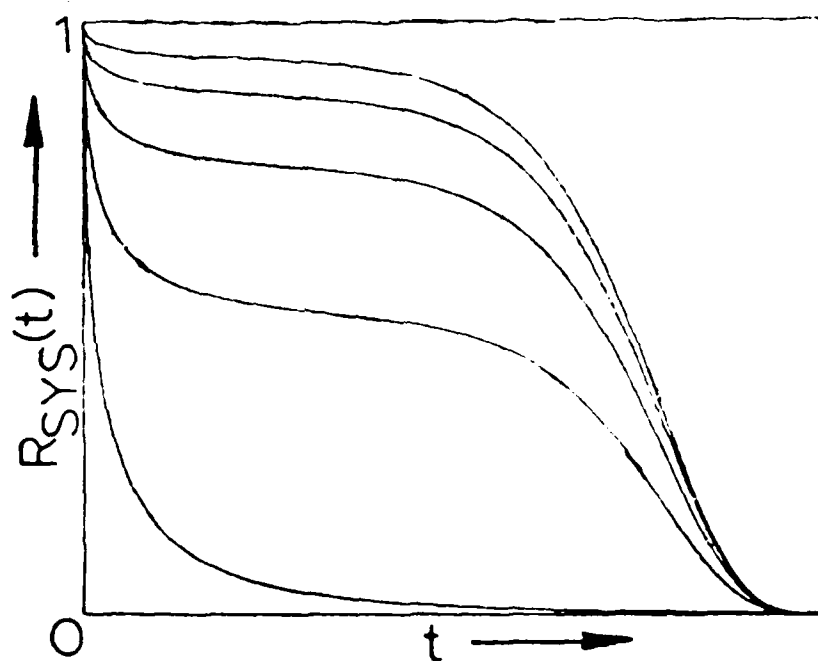
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Figure 3

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Figure 4

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